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REVIEW ARTICLE

Probiotics as beneficial microbes in aquaculture: an update on their multiple modes of action: a review

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ABSTRACT
Wide and discriminate use of antibiotics has resulted in serious biological and ecological concerns, especially the emergence of antibiotic resistance. Probiotics, known as beneficial microbes, are being proposed as an effective and eco-friendly alternative to antibiotics. They were first applied in aquaculture species more than three decades ago, but considerable attention had been given only in the early 2000s. Probiotics are defined as live or dead, or even a component of the microorganisms that act under different modes of action in conferring beneficial effects to the host or to its environment. Several probiotics have been characterized and applied in fish and a number of them are of host origin. Unlike some disease control alternatives being adapted and proposed in aquaculture where actions are unilateral, the immense potential of probiotics lies on their multiple mechanisms in conferring benefits to the host fish and the rearing environment. The staggering number of probiotics papers in aquaculture highlights the multitude of advantages from these microorganisms and conspicuously position them in the dynamic search for health-promoting alternatives for cultured fish. This paper provides an update on the use of probiotics in finfish aquaculture, particularly focusing on their modes of action. It explores the contemporary understanding of their spatial and nutritional competitiveness, inhibitory metabolites, environmental modification capability, immunomodulatory potential and stress-alleviating mechanism. This timely update affirms the importance of probiotics in fostering sustainable approaches in aquaculture and provides avenues in furthering its research and development.

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1. Introduction

The aquaculture industry is rapidly growing and is now considered a major contributor in the global food production. According to the United Nations Food and Agriculture Organization, the growth of aquaculture sector is higher than any other types of animal food production systems (www.fao.org). To meet the global demand, aquaculture production practices have been intensified to a greater extent both in technological and practical measures (Tuan et al. 2013). However, the growth of aquaculture industry is hampered by unpredictable mortalities, many of which are caused by pathogenic microorganisms. Bacterial diseases have been attributed as biological production bottlenecks in intensive aquaculture, hence necessitating the use of chemicals such as drugs and antibiotics in health management strategies (Newaj-Fyzul & Austin 2014). Antibiotic application had been an effective strategy in the beginning, but the residuals remaining in the rearing environment exert selective pressure for long periods of time and became a big challenge (Lakshmi et al. 2013). The indiscriminate use resulted in the emergence of antibiotic-resistant bacteria in aquaculture environments, in the increase of antibiotic resistance in fish pathogens, in the transfer of these resistance determinants to bacteria of land animals and to human pathogens, and in alterations of the bacterial flora both in sediments and in the water column (Verschuere et al. 2000). These alarming disadvantages prompted the aquaculture industry to explore and develop strategies that are as equally effective as antibiotics, eco- and consumer-friendly and most importantly sustainable (Standen et al. 2013; Lazado et al. 2015).

Probiotics is one of the identified alternatives that can lessen the dependence of the aquaculture industry to antibiotics (Verschuere et al. 2000; Nayak 2010; Lazado & Caipang 2014a, 2014b; Akhter et al. 2015). The word *probiotic* originated from the Greece words 'pro' and 'bios' which collectively mean 'for life', hence

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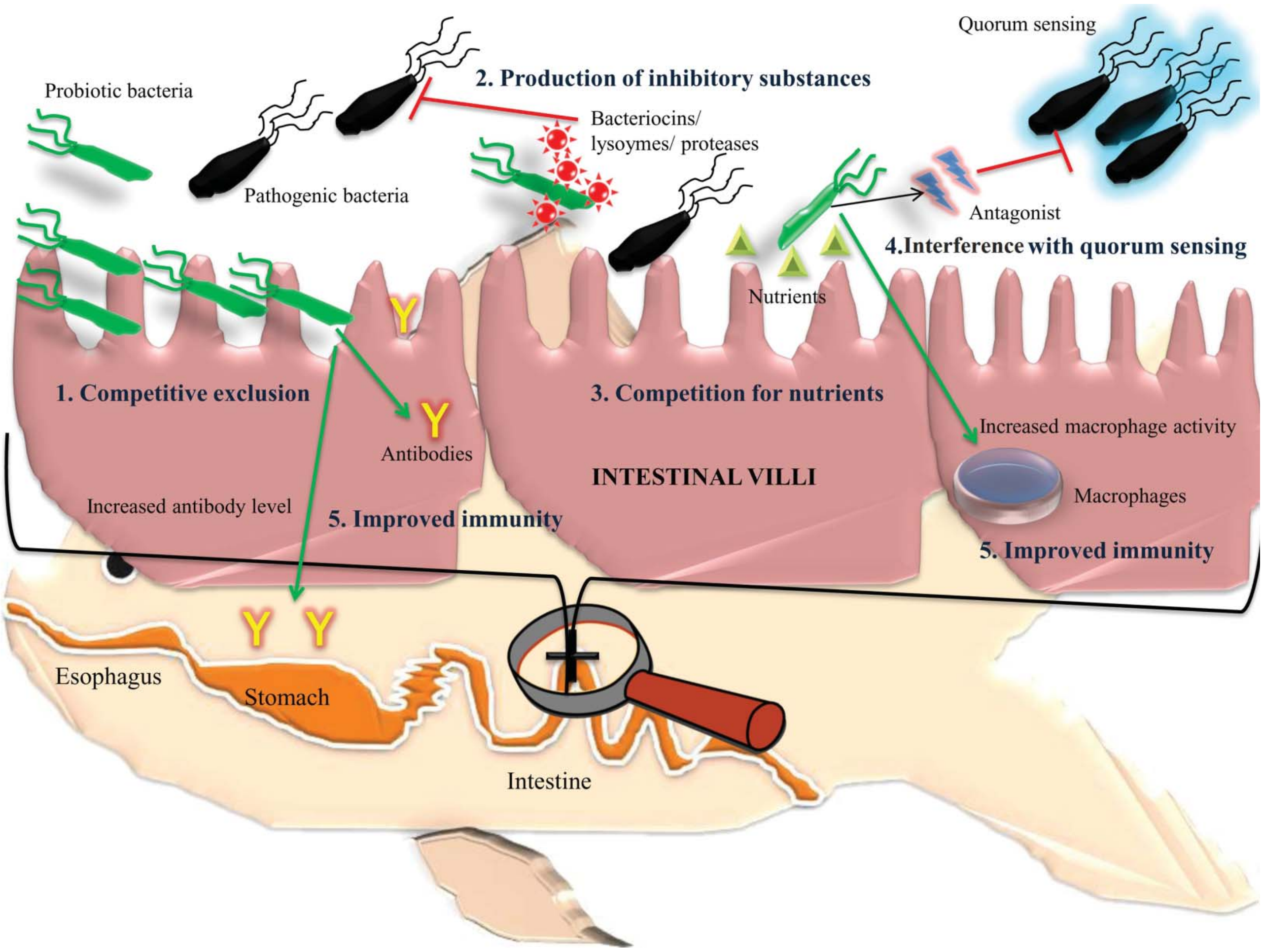

Figure 1. General mechanism of action of probiotics. (1) Competitive exclusion – probiotic organism colonizes the gut thereby inhibiting colonization of pathogenic bacteria. (2) Probiotic organisms produce certain inhibitory substances which hinder pathogenic organism. (3) Competition for nutrients – probiotic organism utilizes the nutrients causing unavailability of nutrients to the pathogens. (4) Substances produced by probiotics act as antagonist for quorum sensing mechanism. (5) Improved immunity – increase macrophage activity and antibody level.

being widely regarded as beneficial microorganisms. For some time, Fuller's definition of probiotics as 'a live microbial feed supplement which beneficially affects the host animal by improving microbial balance' was the adapted understanding of probiotic concept in many cultured animals. Interestingly, the results of probiotics research in aquaculture have opened numerous possibilities on the benefits from this group of microorganisms. Recently, Lazado and Caipang (2014a, 2014b) proposed that probiotics under an aquaculture understanding be defined as 'live or dead, or even a component of the microorganisms that act under different modes of action in conferring beneficial effects to the host or to its environment'. This contemporary definition reflects all the advances in probiotics research in aquaculture for over three decades since its first application.

Probiotics have several mechanisms in conferring their benefits to the host fish (Figures 1 and 2). Such a feature makes probiotic research in aquatic animals a very dynamic field. The results demonstrating the multitude of ways in delivering benefits to the host have immensely expanded the traditional understanding of probiotics as modifier of the microbial community in the host. This paper discusses the immense potential of probiotics as health-promoting alternative through the identified different modes of action of probiotics following their application in finfish aquaculture. It focuses more on how they improve the quality of the rearing environment, protect fish from biological hazards, and modulate physiological processes that eventually promote the health and welfare status of fish in culture. The synthesis provided here collates our current understanding of how probiotics are beneficial to fish and how we can utilize these microorganisms in fostering more sustainable aquaculture practices.

2. Source of probiotics

In the last three decades, several probiotic microorganisms have been identified, characterized and applied in aquaculture. These beneficial microorganisms can be of host or non-host origin (Lazado & Caipang 2014b; Lazado et al. 2015). In a recent review paper, it was highlighted that host-associated microorganisms offer a great prospect as a source of probiotics with diverse biochemical features (Lazado et al. 2015). Bacteria obtained from intestine of aquatic as well as terrestrial animals are commonly used as

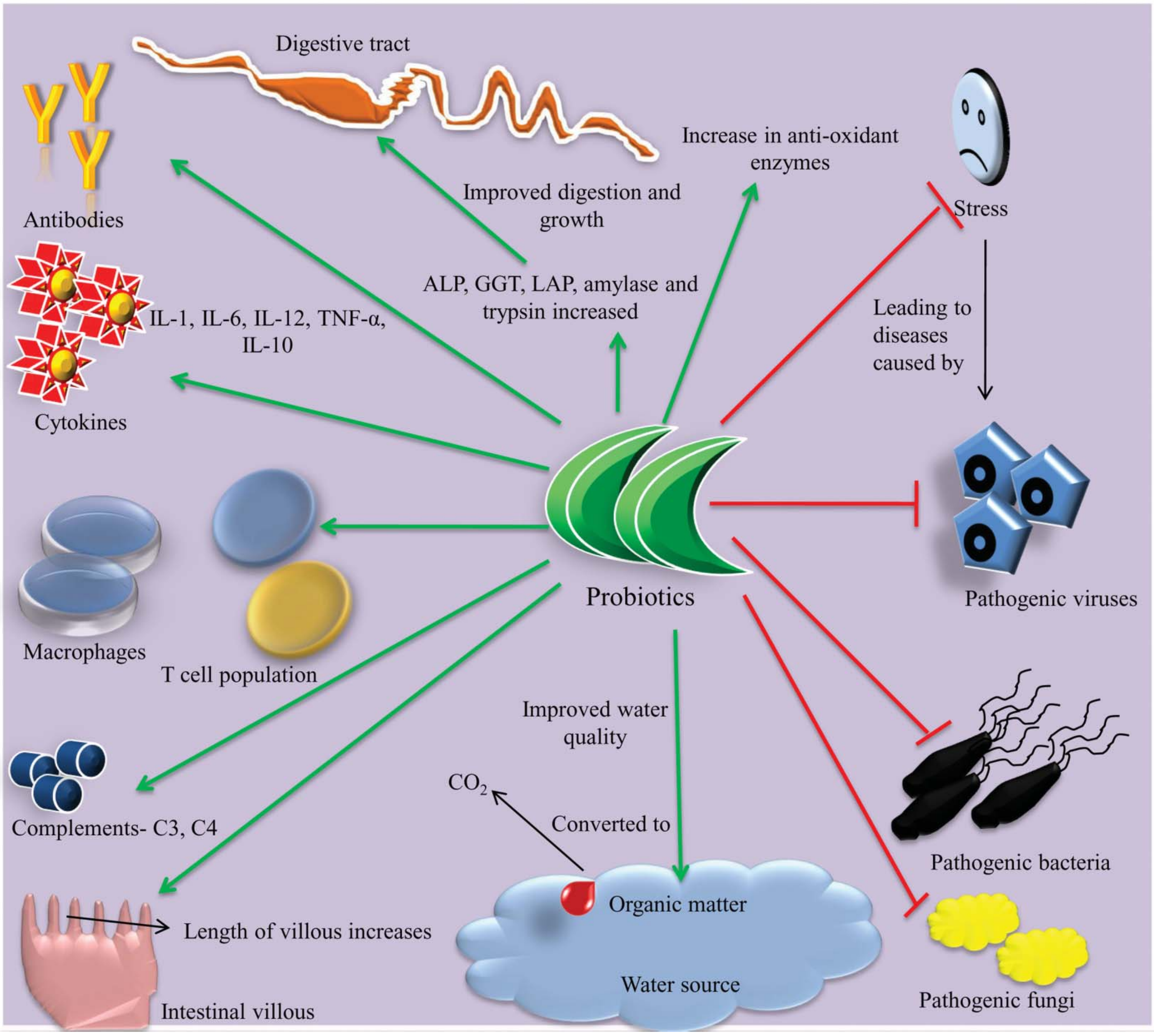

Figure 2. Overall beneficial effects of probiotic in aquaculture. Green arrow indicates additive effects. Red lines indicate inhibitory effect.

probiotics in aquaculture (Hai & Fotedar 2010). Several bacterial species such as *Vibrio* and *Pseudomonas* spp. isolated from marine fishes are being proposed as probiotics. Different species of probiotics used in aquaculture and their beneficial effects are enumerated in Table 1. There is no united stand as to what is the best source of probiotics to be applied for fish. Probiotics from terrestrial environment have been documented conferring numerous benefits to the cultured animals. On the other hand, probiotics of host origin offer several advantages as well, especially a leverage in some biotechnical concerns (i.e. temperature, salinity, familiarity of the environment).

Various factors impose a decisive role in the selection of a suitable probiotic for aquatic species. Different features like type of probiotic (i.e. bacteria, fungi or algae), host from which they are derived (i.e. host or non-host), single-strain probiotic or multi-strain, use of either viable or non-viable organisms as probiotic and also use of spore formers or non-spore formers was used in aquaculture (Nayak 2010). These are some of the reasons why having probiotics of universal application seems impractical.

The most commonly used probiotic species include genera *Lactobacillus*, *Bifidobacterium*, *Aeromonas*, *Plesiomonas*, *Bacteroides*, *Fusubacterium*, *Carnobacterium* and *Eubacterium* and strains of *Bacillus*, *Enterococcus*, *Bacteroides*, *Clostridium*, *Agrobacterium*, *Pseudomonas*, *Brevibacterium*, *Microbacterium*, *Staphylococcus*, *Streptomyces*, *Micrococcus*, *Psychrobacter*, *Carnobacterium*, *Pediococcus*, *Saccharomyces*, *Debaryomyces*, *Altermonas*, *Tetraselmis*, *Roseobacter*, *Weissella* and *Aspergillus* (Balcazar et al. 2006; Nayak 2010; Lakshmi et al. 2013; Tuan et al. 2013; Lazado et al. 2015).

3. Modes of action

3.1. Competition for space

Many of the pathogenic bacteria require attachment to the mucosal layer of the host gastrointestinal tract to

Table 1. Different species of probiotics used in aquaculture and their beneficial effects.

No.	Probiotic candidates	Aquatic species in which probiotics are used	Beneficial effects	References
Gram-negative bacteria				
1	*Aeromonas hydrophila*	*Oncorhynchus mykiss* (Rainbow trout)	*Aeromonas salmonicida* infection reduced	Irianto and Austi (2002a, 2002b)
2	*Aeromonas media* A199	*Crassostrea gigas* (Pacific oyster)	Reduced *Vibrio tubiashii* infection	Gibson (1999)
3	*Aeromonas sobria* GC2	Rainbow trout	Protection against *Lactococcus garvieae* and *Streptococcus iniae.* Similarly protects against *Aeromonas bestiarum* (causative of fin rot) and *Ichthyophthirius multifiliis* (skin parasite)	Pieters et al. (2008); Brunt and Austin (2005)
4	*Agarivorans albus* F1-UMA	*Haliotis rufescens* (Abalone)	Survivability increased	Silva-Aciares et al. (2011)
5	*Alteromonas* CA2	Pacific oyster	Survivability increased	Douillet and Langdon (1994)
6	*Alteromonas macleodii* 0444	*Perna canaliculus* (Greenshell mussel)	Controls *Vibrio splendidus* infection	Kesarcodi-Watson et al. (2010, 2012)
		Pecten maximus (Scallop)	Controls *Vibrio coralliilyticus* and *V. splendidus*	
7	*Burkholderia cepacia* Y021	*Crassostrea corteziensis* (Cortez oyster), *Nodipecten subnodosus* (Lions-pay scallop)	Increased growth and survival	Granados-Amores et al. (2012)
8	*Enterobacter amnigenus*	Rainbow trout	Increased resistance towards *Flavobacterium psychrophilum*	Burbank et al. (2011)
9	*Neptunomonas* 0536	*Perna P. canaliculus* (Greenshell mussel)	*V. splendidus* infection controlled	Kesarcodi-Watson et al. (2010, 2012)
10	*Pseudomonas aeruginosa, P. synxantha*	*Penaeus latisulcatus* (Western king prawns)	General health and immune status improved	Hai et al. (2009)
11	*Shewanella putrefaciens*	*Sparus aurata L.* (Gilthead sea bream)	Improved growth of juveniles	De la Banda et al. (2012)
Gram-positive bacteria				
12	*Arthrobacter* XE-7	*L. vannamei* (Pacific white shrimp)	Alters intestinal microbes	Li et al. (2008)
13	*Bacillus circulans* PB7	*Labeo rohita* (Rohu)	Act as immune stimulant and protects against *A. hydrophila*	Bandyopadhyay and Das Mohapatra (2009)
14	*Bacillus subtilis* and *Bacillus licheniformis*	Trout	Protects against *Yersinia ruckeri*, FCR and growth improved	Raida et al. (2003)
15	*B. subtilis*	*Labeo rohita* (Indian major carp)	Controls *A. hydrophila*	Kumar et al. (2006)
		White shrimp	Immunity increased and resistance against *V. harveyi* increased	Zokaeifar et al. (2012)
		Ictalurus punctatus (Channel cat fish) and *Pangasianodon hypophthalmus* (Striped cat fish)	Decreased mortality rate due to *Edwardsiella ictaluri*	Ran et al. (2012)
16	*B. subtilis* UTM 126	*Litopenaeus vannamei* (White shrimp)	Protection against vibriosis	Das et al. (2006)
17	*B. subtilis* E20	*Litopenaeus vannamei* (White shrimp)	Mortality reduced	Liu et al. (2010)
18	*Bacillus megaterium*	Shrimp	Immunity improved, intestinal microbes altered and resistant to white spot syndrome virus	Li et al. (2009)
19	*Bacillus pumilus*	*P. japonicus*	Improved larval survival	El-Sersy et al. (2006)
		O. niloticus (Tilapia)	Immunity increased and survivability increased against *A. hydrophila* challenge	Aly et al. (2008a)
20	*Bacillus* P64	*L. vannamei* (White shrimp)	Immunostimulant	Gullian et al. (2004)
21	*Bacillus* 48	*Centropomus undecimalis* (Common snook)	Growth improved	Kennedy et al. (1998)
22	*Brevibacillus brevis*	*Dicentrarchus labrax* (Sea bass)	Prevent vibriosis and improve growth	Mahdhi et al. (2012)
23	*Brochothrix thermosphacta* BA211	Rainbow trout	Protect against *A. bestiarum*	Pieters et al. (2008)
24	*Clostridium butyricum*	Rainbow trout	Protect against vibriosis and also from *A. hydrophila* and *V. anguillarum* infections	Sakai et al. (1995)
		Miichthys miiuy (Chinese drum)	Increased immunity and disease resistance	Pan et al. (2008)
25	*Carnobacterium divergens*	*Gadus morhua* (Atlantic cod), Atlantic salmon (*Salmo salar*) and rainbow trout (*O. mykiss*)	Protects against *V. anguillarum* infection	Gildberg et al. (1997); Robertson et al. (2000)
26	*Enterococcus faecium* SF 68	*Anguilla anguilla* (European eel)	Prevents against Edwardsiellosis	Chang and Liu (2002)
27	*E. faecium* MC13	*Penaeus monodon* (Shrimp)	Protects against *V. harveyi* and *V. parahaemolyticus*	Swain et al. (2009)
28	*Kocuria* SM1	Rainbow trout	Protects against *V. anguillarum* and *V. ordalii*	Sharifuzzaman and Austin (2010)
29	*Lactobacillus acidophilus*	Nile tilapia	Immunity increased and protects against *P. fluorescens* and *S. iniae*	Aly et al. (2008b)
30	*L. acidophilus*	*Clarias gariepinus* (African catfish)	Growth performance, haematological parameters and immunoglobulin concentration	Al-Dohail et al. (2009)
30	*Lactobacillus rhamnosus* ATCC 53101	Rainbow trout	Reduction in mortality caused by A. salmonicida	Nikoskelainen et al. (2001)
31	*L. rhamnosus*	*O. niloticus*	Protects against *E. tarda* infection	Pirarat et al. (2006)

(*continued*)

Table 1. (*Continued*)

No.	Probiotic candidates	Aquatic species in which probiotics are used	Beneficial effects	References
32	*Lactobacillus fructivorans* and *L. plantarum*	*S. aurata* (Sea bream)	Increase in production of HSP70, thereby increasing heat tolerance	Carnevali et al. (2004); Rollo et al. (2006)
33	*Lactococcus lactis* AR21	Rotifers	Improved growth and protects against *V. anguillarum* infection	Harzevili et al. (1998)
	Lactobacillus sporogenes	*Macrobrachium rosenbergii* (Freshwater prawn)	Boosts the survival, growth and levels of biochemical constituents	Seenivasan et al. (2012)
34	*Leuconostoc mesenteroides* CLFP 196 and *L. plantarum* CLFP 238	Rainbow trout	Mortality due to *L. garvieae* was reduced	Vendrell et al. (2008)
35	*Micrococcus luteus*	*O. mykiss* (Rainbow trout)	Infection due to *A. salmonicida* was reduced	Irianto and Austin (2002a)
36	*Micrococcus* MCCB 104	*M. rosenbergii* (Fresh water prawn)	Different bacteria inhibited	Jayaprakash et al. (2005)
37	*Pediococcus acidilactici*	Rainbow trout fry	Vertebral column compression syndrome (VCCS) was reduced	Aubin et al. (2005)
38	*Rhodococcus* SM2	Rainbow trout	Immunity improved and protection against *V. anguillarum*	Sharifuzzaman et al. (2011)
39	*Streptococcus phocae* P180	*P. monodon*	Growth increased and protects against *V. harveyi* infection	Swain et al. (2009)
40	*Streptococcus faecium*	*Oreochromis niloticus* (Nile tilapia)	As growth promoters	Lara-Flores et al. (2003)
41	*S. Faecium*	*Cyprinus carpio* (Carp)	Improves growth and intestinal micro flora	Bogut et al. (1998)
41	*Streptomyces*	*P. monodon*	Growth improved and water quality was also increased	Das et al. (2006); Newaj-Fyzul et al. (2014)
42	*Vagococcus fluvialis*	Sea bass	Protection against *V. anguillarum* infection	Sorroza et al. (2012)
43	*Weissella hellenica* DS-12	–	Protects against several fish pathogens	Byun et al. (1997); Cai et al. (1998)
Phages and yeast				
44	Phages of family Myoviridae and Podoviridae	*Plecoglossus altivelis*	Protection against *Pseudomonas plecoglossicida*	Park et al. (2000)
45	Microaglae *Tetraselmis suecica*	Penaeids	Protection against bacterial pathogen	Austin and Day (1990)
46	*Dunaliella tertiolecta*	*Artemia*	Protection against *Vibrio campbellii* and *V. proteolyticus*	Marques et al. (2006)
47	Yeasts (*Phaffia rhodozyma, Saccharomyces cerevisiae* and *Saccharomyces exiguous*)	Penaeids	Protection against vibriosis	Scholz et al. (1999)
48	*Yarrowia lipolytica*	Pinctada *mazatlanica*	Improved growth	Aguilar-Macias et al. (2010)

initiate the development of a disease (Adams 2010). An important mechanism of action in probiotic bacteria is competition for adhesion sites, also known as 'competitive exclusion'. The ability of bacteria to colonize the gut and adhere to the epithelial surface and consequently interfere with the adhesion of pathogens is a desirable criterion in the selection of probiotics (Balcazar et al. 2006; Lazado et al. 2011). Non-pathogenic intestinal microbes such as *Lactobacilli* compete with the pathogens for adhesion sites on the intestinal surfaces, particularly on intestinal villus and enterocytes (Brown 2011).

Probiotic addition is being suggested as an early stage husbandry practice in larviculture because the feature of competitive exclusion for attachment sites could provide favorable rearing conditions (Irianto & Austin 2002a). Attachment of probiotics may be non-specific, based on the physicochemical agents, or specific, based on the adhesion of the probiotics on the surface of the adherent bacteria and receptor molecules on the epithelial cells (Salminen et al. 1996; Lazado et al. 2015).

3.2. Production of inhibitory substances

Probiotic bacteria produce substances with bactericidal or bacteriostatic effects on other microbial populations (Servin 2004) such as bacteriocins, hydrogen peroxide, siderophores, lysozymes, proteases, among many others (Panigrahi & Azad 2007; Tinh et al. 2007). In addition, some bacteria produce organic acid and volatile fatty acids (e.g. lactic, acetic, butyric and propionic acids), that can result into the reduction of pH in the gastrointestinal lumen, thus preventing growth of opportunistic pathogenic microorganisms (Tinh et al. 2007).

Recently, a compound called indole(s,3-benzopyrrole) with potent inhibitory activity against pathogens was identified in some bacteria known to have antibacterial and anti-fungal activities (Gibson et al. 1999; Lategan et al. 2006).

3.2.1. Antibacterial activity

Several probiotics in aquaculture have been documented possessing antibacterial activity against known pathogens. For example, probiotic *L. lactis* RQ516 that is being used in tilapia (*Oreochromis niloticus*) exhibited inhibitory activity against *Aeromonas hydrophila* (Zhou et al. 2010). It was also shown by Balcázar et al. (2008) that probiotic *L. lactis* had antibacterial activity towards two fish pathogens namely, *Aeromonas salmonicida* and *Yersinia rukeri*.

Zapata and Lara-Flores (2013) found that *Leuconostoc mesenteroides* was able to inhibit the growth of fish pathogenic bacteria in Nile tilapia (*O. niloticus*). Ghosh et al. (2008) found that *Bacillus subtilis* significantly reduced the amount of motile *Aeromonads*, presumptive *Pseudomonads* and total Coliforms in ornamental fishes (Newaj-Fyzul & Austin 2014). Moosavi-Nasab et al. (2014) also reported that lactic acid bacteria (*Lactobacillus buchneri*, *Lactococcus lactis*, *Lactobacillus acidophilus*, *Lactobacillus fermentum* and *Sterptococcus salivarius*) isolated from the intestine of Spanish mackerel (*Scomberomorus commerson*) were able to inhibit the growth of *Listeria innocua*. Dhanasekaran et al. (2008) reported that several *Lactobacilli* isolated from intestine of catfish (*Clarias orientalis*), Hari fish (*Anguilla* sp.), Rohu fish (*Labeo rohita*), Jillabe fish (*Oreochromis* sp.) and Gende fish (*Punitus carnaticus*) showed remarkable antibacterial activity against *Aeromonas* and *Vibrio* sp.

The potential of probiotic including *Lactobacillus plantarum* (LP1, LP2), *Saccharomyces cerevisiae* (SC3), *Candida glabrata* (CG2), *L. lactis* subsp. lactis (LL2) and *Staphylococcus arlettae* (SA) isolated from an indigenous fish sauce in Malaysia showed high inhibitory activity on *Staphylococcus aureus* and *Listeria monocytogenes* (Dhanasekaran et al. 2008).

3.2.2. Antiviral activity

The knowledge on antiviral activity of probiotics has been raised in recent years (Lakshmi et al. 2013). For example, *Pseudomonas*, *Vibrio*, *Aeromonas* spp. and *Coryneforms* had antiviral activity against infectious hematopoietic necrosis virus (IHNV) (Kamei et al. 1988). Li et al. (2009) demonstrated that feeding with a *Bacillus megaterium* strain increased the resistance to white spot syndrome virus (WSSV) in the shrimp *Litopenaeus vannamei*. It was documented that probiotics such as *Bacillus* and *Vibrio* sp. positively protect shrimp *L. vannamei* against WSSV (Balcazar 2003). Application of *Lactobacillus* probiotics as a single strain or mixed with Sporolac improved disease resistance against lymphocystis viral disease in olive flounder (*Paralichthys olivaceus*) (Harikrishnan et al. 2010).

3.2.3. Antifungal activity

There are few studies regarding the antifungal effect of probiotics. Lategan et al. (2004) isolated *Aeromonas media* (strain A199) from eel (*Anguilla australis*) culture water and was observed to have a strong inhibitory activity against *Saprolegnia* sp. In a separate study, *Pseudomonas* sp. M162, *Pseudomonas* sp. M174 and *Janthinobacterium* sp. M169 enhanced immunity against saprolegniasis in rainbow trout. Atira et al. (2012) demonstrated that *L. plantarum* FNCC 226 exhibited inhibitory activity against *Saprolegnia parasitica* A3 in catfish (*Pangasius hypophthalamus*).

3.3. Competition for chemicals or available energy

The existence of any microbial population depends on its ability to compete for chemicals and available energy with the other microbes in the same environment (Verschuere et al. 2000). Many microorganisms, including the known probiotic group lactic acid bacteria, consume the nutrients that are essential for the growth of a number of pathogens (Brown 2011).

For example, siderophores are low-molecular-weight ferric iron-chelating agents that are able to dissolve precipitated iron or extract it from iron complexes, then making it available for bacterial growth (Neilands 1981). Siderophore-producing bacteria can be used as probiotics because they can sequester ferric iron in an iron-low environment, hence making it unavailable for the growth of pathogenic bacteria (Tinh et al. 2007). Gram et al. (1999) showed that a culture supernatant of *Pseudomonas fluorescens*, grown in iron-limited conditions, inhibited growth of *Vibrio anguillarum*. It has been shown that *P. fluorescens* can competitively inhibit the growth of the fish pathogen *A. salmonicida,* by competing for free iron (Smith & Davey 1993; Gram et al. 1999). It was also revealed that GP12 and GP21, candidate probiotics from Atlantic cod, are capable of releasing sideropheres and this ability had been implicated for their beneficial use (Lazado et al. 2011).

3.4. Improving the water quality

Application of Gram-positive bacteria, such as *Bacillus* spp., is beneficial in improving the quality of the water system. *Bacillus* spp. have a more efficient ability in converting organic matter into carbon dioxide in comparison to the Gram-negative bacteria, which converts a greater proportion of organic matter into bacterial biomass or slime (Balcazar et al. 2006; Mohapatra et al. 2012). Certain probiotic bacteria possess significant algicidal effect as well particularly on several species of microalgae (Fukami et al. 1997). Ammonia and nitrite toxicity can be eliminated by the application of nitrifying cultures into the fish environment (Mohapatra et al. 2012). In addition, probiotics are beneficial as they can increase microbial species' composition in the water and modify its quality (Mohapatra et al. 2012). The temperature, pH, dissolved oxygen, NH_3 and H_2S in rearing water were found to be of higher quality when probiotics were added, hence maintaining a positively healthy environment for shrimp and prawn larval in green water system (Banerjee et al. 2010; Aguirre-Guzman et al. 2012).

3.5. Nutrients and enzymatic contribution

Some microorganisms have a positive effect in the digestive processes of aquatic animals (Balcazar et al. 2006). It has been shown that some bacteria contribute in the digestion process by producing extracellular enzymes, such as proteases, lipases, as well as growth-promoting factors (Wang et al. 2000).

There are reports demonstrating that some probiotics, especially from *Bacteroides* and *Clostridium* sp., are capable of supplying vitamins, fatty acids and essential amino acids to the host (Balcazar et al. 2006; Tinh et al. 2007). Gnotobiotic oyster larvae (*Crassostrea gigas*), fed with auxenic algae (*Isochrysis galbana*) supplemented with a bacterial strain CA2, showed not only improved growth performance but efficient nutrient utilization as well (Douillet & Langdon 1994). Yeasts are well known in animal nutrition because they can produce polyamines, which enhance intestinal maturation (Wang et al. 2000). Besides bacterial probiotics, many strains of yeast have been used as dietary supplements in a number of fish species (Tinh et al. 2007).

3.6. Interference of quorum sensing

Quorum sensing (QS) is defined as the regulation of gene expression in response to fluctuations in cell-population density. Many bacteria are using this system to communicate and regulate a diverse array of physiological activities (Miller & Bassler 2001). The disruption of QS is considered a potential anti-infective strategy in aquaculture (Defoirdt et al. 2004).

Halogenated furanones, which are produced by the marine red alga *Delisea pulchra* (Manefield et al. 1999), have been investigated as a promising QS antagonist. These compounds, added at adequate concentrations, protected Brachionus, Artemia, and rainbow trout from the negative effects of pathogenic *Vibrios* (Rasch et al. 2004; Defoirdt et al. 2006; Tinh et al. 2007). Also, some probiotic bacteria such as *Lactobacillus*, *Bifidobacterium* and *Bacillus cereus* strains degrade the signal molecules of pathogenic bacteria by enzymatic secretion or production of autoinducer antagonists (Brown 2011). It was demonstrated by Medellin-Pena et al. (2007) that *L. acidophilus* secretes a molecule that inhibits the QS or interacts with bacterial transcription of *Escherichia coli* O157 gene.

3.7. Immunomodulation

3.7.1. Fish

Probiotics by stimulation of immune system of hosts, including the stimulation of pro-inflammatory cytokines on the activity of immune cells, increasing the phagocytic activity of leucocytes (Pirarat et al. 2006), increasing the levels of antibodies, acid phosphatase, lysozymes (Lara-Flores & Aguirre-Guzman 2009), complement (Balcazar et al. 2007), cytokines (interleukin-1 (IL-1), IL-6, IL-12, tumor necrosis factor α (TNF-α), gamma interferon (IFN-γ), IL-10 and transforming growth factor b) (Nayak 2010) and antimicrobial peptides (Mohapatra et al. 2012), and also, by improving the intestinal microbial balance, inhibiting the colonization of fish pathogens in the digestive tract, producing of inhibitory compounds such as bacteriocins, siderophers, lysozymes, proteases, hydrogen peroxides (Saurabh et al. 2005), increasing the digestive enzymes activity (amylase, protease and lipase) (Ringø et al. 1995) and by producing of fatty acids, vitamins (Sakata 1990) and essential amino acids that are useful for lactic acid bacteria (Ringø & Gatesoupe 1998) could improve the growth performance, immune system and increased resistance on common pathogens in fish and shrimp (Lakshmi et al. 2013).

In a study, administration of probiotics in tilapia (*O. niloticus*) caused increase in lysozyme activity, neutrophil migration, bactericidal activity and finally enhanced resistance of fish to infection of *Edwardsiella tarda* (Taoka et al. 2006b). Also, Gomez et al. (2007) used *Vibrio alginolyticus* strains as probiotics in white shrimp (*L. vannamei*) and observed increased survival and growth in shrimp (Zhou et al. 2009).

Harikrishnan et al. (2011a) reported that administration of probiotics (*Lactobacillus sakei* BK19) with herb (*Scutellaria baicalensis*) in tilapia (*O. fasciatus*) reduces the mortality, alters haematological parameters and enhances innate immunity against *E. tarda*. The same researchers repeated this experiment in olive flounder (*P. olivaceus*) against *Streptococcus parauberis* and found improved growth, blood biochemical constituents, and nonspecific immunity in the groups treated with probiotics and herbals mixture supplementation diet (Harikrishnan et al. 2011b). Irianto and Austin (2002a) reported that feeding with Gram-positive and Gram-negative probiotics resulted in the stimulation of cellular rather than humoral (serum of mucus antibodies) immunity. There was an increase in the number of erythrocytes, macrophages and lymphocytes, and enhanced lysozyme activity during feeding with probiotics. Feeding with diets containing single or mixed isolated probiotic bacteria for *O. niloticus* showed different results in survival rates and was highest with fish fed diets supplemented with *Bacillus pumilus*, followed by a mixture of probiotics (*B. firmus, B. pumilus* and *Citrobacter freundii*), and then *C. freundii*

Avella et al. (2010) used a mixture of *Bacillus* probiotic bacteria including *B. subtilis*, *B. licheniformis* and *B. pumilus* in diet of the gilthead sea bream (*Sparus aurata*) larviculture and observed clear effects on survival, growth and general welfare.

In a research, first, fish were fed the diet containing *L. plantarum*. Assessment of mRNA levels of several immune parameters like cytokine IL-8 in the intestine of the control and *L. plantarum* groups by using real-time PCR showed that IL-8 gene expression was significantly upregulated by *L. plantarum* after *Lactococcus garvieae* infection (Pérez-Sánchez et al. 2011). Standen et al. (2013) evaluated the probiotic effect of *Pediococcus acidilactici* on Nile tilapia (*O. niloticus*) and suggested that the probiotic treatment may cause upregulation of the gene expression of the proinflammatory cytokine TNF-α in the probiotic fed fish. Presence of *B. subtilis* C-3102 in the diets of hybrid tilapia juvenile (*O. niloticus* $\times$ *O. aureus*) caused upregulation of cytokines such as IL-1β, TGF-β, and TNF-α in the intestine of fish (He et al. 2013). *Lactobacillus delbrueckii* ssp. *delbrueckii* (AS13B) added in the diet of gilthead sea bream resulted in lower transcription of proinflammatory cytokine genes such as IL1β, IL10, cox2 and TGF-β in the intestine of treated group (Picchietti et al. 2009).

3.7.2. Shrimp

Use of probiotics in different species of shrimps has improved the innate immunity (natural or non-specific immunity). Several studies have demonstrated that by using probiotics the production of cellular components such as phagocytosis, encapsulation, formation of nodules and humoral components including anticoagulant proteins, agglutinins, phenol oxidase enzyme (Lakshmi et al. 2013; Song et al. 2014), antimicrobial peptides (defensins and chemokines), antiapoptotic protein, free radicals, bacteriocins, siderophores, monostatin, lysozymes, proteases, hydrogen peroxide, gramicidin, polymyxin, tyrotricidin, competitive exclusion and organic acid was increased (Balcazar et al. 2007). Probiotics have an important role to enhance the resistance of shrimps against common diseases such as vibriosis, white spot disease and *A. hydrophila* infection (Ahilan et al. 2004; Ma et al. 2007; Harikrishnan et al. 2009; Liu et al. 2010; Zokaeifar et al. 2014).

It was also confirmed by RNA interference (RNAi) assay that the immunity of shrimps was increased against viral diseases, using probiotics (Kawai & Akira 2006). Rangpipat et al. (2000) showed that *Bacillus* sp. (strain S11) provided protection against disease by activating the *Penaeus monodon* immune system.

3.7.3. Immunomodulation of the gut immune system

The immune system of the gut is related to gut-associated lymphoid tissue (GALT) (Nayak 2010; Lazado & Caipang 2014a, 2014b) and there are some differences in respect of Peyer's patches, secretory IgA and antigen-transporting M cells in the intestine of piscine and mammal gut immune system (Nayak 2010). Although lymphoid cells, macrophages, granulocytes and mucus IgM were observed in the intestine of fish, the effect of probiotics on the intestinal immune cells is less known (Bakke-McKellep et al. 2007; Nayak 2010).

There is limited knowledge about application of probiotics and their ability in stimulating the piscine gut immune system (Nayak 2010; Lazado & Caipang 2014a, 2014b). The present knowledge is mostly associated with humans and terrestrial vertebrates (Lazado & Caipang 2014a, 2014b). However, studies indicated that probiotics can stimulate the piscine gut immune system, increasing the number of Ig^{+}-cells and acidophilic granulocytes (AGs) (Picchietti et al. 2007, 2008, 2009; Salinas et al. 2008). For example, it has been reported that the supplementation of LAB (*Lactobacillus rhamnosus* GG, human origin) in diet of tilapia, *O. niloticus* could modulate the population of the intestinal immune cells. Also, the amount of intra-epithelial lymphocytes and AGs enhanced significantly in the probiotic-fed group (Pirarat et al. 2011). Addition of probiotic containing *Lactobaccillus fructivorans* (host origin) and *L. plantarum* (human origin) to the diet of larval gilthead sea bream, *S. aurata*, by live vectors affected the extent of Ig^{+}-cells and AGs, mostly the MAb G7(+) phagocytic population in gut (Picchietti et al. 2007).

Picchietti et al. (2009) used rotifers and artemia in administration of *L. delbrueckii* ssp. *delbrueckii* (AS13B) as live vectors to the larval sea bass, *Dicentrarchus labrax*. They observed the population of T-cells and AGs in the intestinal mucosa significantly increased in probiotic-fed fish.

In a study, rainbow trout (*Oncorhynchus mykiss*) were fed by diets supplemented with probiotics such as *L. lactis* spp. *lactis*, *L. mesenteroides* and *L. sakei*. At the end, an enhancement was observed in phagocytic activity of mucosal leucocytes by LAB group (Balcazar et al. 2006). *Pediococcus acidilactici* was used by Standen et al. (2013) in the feeding of Nile tilapia (*O. niloticus*).

3.8. Amelioration of the effects of stress

Stress might be regarded as a physical or chemical agent causing reactions that may result in disease and death. Any change in water parameters may have a side effect on the physiological and behavioral aspect of aquatic animals. Different types of stress that may have negative effects on fish include thermal (Das et al. 2005; Logan & Somero 2011), nutritional, high density (Lupatsch et al. 2010), anoxia, hypoxia, chemicals and toxins (DeMicco et al. 2010). Many harmful agents for fish exist in their environment like the water, soil, air or even their own body (Smith et al. 2012). In intensive systems of aquaculture where the high density is an important factor for outbreak, in stressful conditions, aquatic animals are more susceptible than wild fishes. Application of probiotic bacteria, both as a feed supplement and water can prevent stressful conditions, enhancing immune system and therefore reducing the harmful effects of various stressors (Taoka et al. 2006a).

Any situation that enhances reactive oxygen species (ROS) concentration is called oxidative stress that can lead to disturbing cellular metabolism and its regulation, thereby damaging cellular constituents (Jia et al. 2011; Lushchak 2011). ROS production is nearly related to antioxidant responses (Lesser 2006; Bidhan et al. 2014). The alterations of temperature and other environmental parameters can severely affect physiological activities of aquatic animals (Wabete et al. 2008). In addition, a wide range of contaminants (xenobiotics), UV radiation, hypoxia and other environmental physicochemical parameters may cause oxidative stress in the animal (Mohapatra et al. 2012). Feeding with probiotics may ameliorate the effects of these oxidative stress factors by increasing the antioxidant status (Mohapatra et al. 2012).

Blood glucose, cortisol and the RNA/DNA ratio of the different tissues are used as valid biochemical stress indicators to study the fish stresses, growth and health status (Sivaraman et al. 2012). Another way to assess stress tolerance in fish involves subjecting them to heat shock (Cruz et al. 2012).

Taoka et al. (2006a) grew flounder (*P. olivaceus*) under stress conditions and evaluated the effects of probiotics on growth, stress tolerance and non-specific immune response in fish. Plasma lysozyme activity in the probiotic diet group and the water supply group was significantly higher than in the control group. In heat shock stress tests, flounder in the probiotics-treated groups showed greater heat tolerance. Koninkx and Malago (2008) demonstrated that under stress conditions, normal intestinal micro flora taken as probiotics were able to enhance defense system by increasing specifically the putative heat shock protein (HSP).

Some probiotic bacteria have been found to decrease several biochemical stress indicators. There is a report regarding the decrease in cortisol level on supplementation of *L. delbrueckii* ssp. *delbrueckii* in the diet of European sea bass (*D. labrax*) compared to the controls during temperature stress (Carnevali et al. 2006).

Taoka et al. (2006a) found that administration of *Bacillus* spp. during transport reduced handling stress by influencing the cortisol level. Varela et al. (2010) carried out probiotic administration studies on gilt-head bream (*S. aurata*) and concluded that there was improved tolerance to stress with this treatment under high stocking density. Castex et al. (2009) evaluated the antioxidative effect of *P. acidilactici* MA 18/5 in shrimp, *Litopenaeus stylirostris*. Results showed the modulation of the activities of antioxidant enzymes such as superoxide dismutase and catalase. It has been reported that administration of *L. plantarum* could enhance the antioxidant state in shrimp *L. vannamei* and consequently improve resistance to *V. alginolyticus* infection (Chiu et al. 2007).

4. Side effects and misuses

Probiotics are generally considered safe and well tolerated (Boyle et al. 2006). One theoretical concern associated with probiotics includes the potential for these viable organisms to move from the gastrointestinal tract and cause systemic infections (Snydman 2008). Another theoretical risk associated with probiotics involves the possible transfer of antibiotic resistance from probiotic strains to pathogenic bacteria; however, this has not yet been observed (Martin et al. 2013). Also, by introduction of probiotics importation in the aquaculture industry, possibilities of change in intestinal microflora, emerging diseases, mutagenesis or recombination of DNA of bacteria may result into systemic infections and economical losses in fish farms (Ringø et al. 2010).

5. Conclusion and future perspectives

Despite doing many studies about efficiency and mechanisms of probiotics, there are many questions that are not yet clear. Additional and future studies can be directed to transcriptome and proteome profiling of gut microbiota, host/microbe interactions, interactions between gut microbes, the intestinal epithelium, gut immune system, antioxidant status, lipid level of hosts, antagonistic and synergist activity or probably side effects of probiotics.

Aquaculture holds an important place among the fastest developing growth sectors globally and contributes about 90% of the world production. Aquaculture provides an important source of fishes with nutritional security for human consumption but infections and disease outbreaks in large aquaculture industry affect both socio-economic status and economic advancement of the country. As therapeutic regimen antibiotics used pose some negative impacts such as residual toxicity, emerging drug resistance, immune suppression and reduced consumer preference for drug-treated aquatic products in the market, hence demand for non-antibiotic-based, environmentally friendly agents is highly desired for health management in aquaculture. Use of probiotics is an effective alternative sustainable source of beneficial microbes with bactericidal or bacteriostatic effect on pathogenic bacteria, with anti-bacterial, anti-viral and anti-fungal activity, immunomodulatory capabilities of promoting health and welfare to improve the growth performance, augment the immune system, disruption of QS as a new anti-infective strategy, ameliorate the harmful effects of oxidative stress factors and increased resistance for common pathogens in fishes for controlling potential fish pathogens. An interactive approach among academicians, scientists, producers and fish sector owners is required to focus and explore the specific aspects of bacteria–host interactions conferring the possible favorable changes in diverse immune responses elicited by different bacterial strains in order to propose clinically effective, bacteria-based strategies to promote the health, production and economic growth of the aquaculture industry. Probiotic formulation should be viable on large scale at low operational cost. They should not be treated as 'elixir of life', rather they should be used as supplement to balance the diet to avail and maintain the sound health free of infections and disease-causing microorganisms. The present review has summarized the importance of potential probiotics and their future perspectives in fastest growing food production sector of aquaculture industry.

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